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1.   Some Essentials of Neural Memory Systems

This report covers research done during June 1962 –
June 1963, and in this period there has been a major
clarification in thinking about the mechanisms by which
the brain is able rapidly to acquire information as to
which lines of behaviour are likely to prove advantageous.
Essentially there are four parts to the system:

1)   Receptor analysers consisting of classifying cells
each set to respond to features of the environment that
are likely to be relevant (e.g., brightness, extent of
horizontal contour),

2)   Switching systems by which each classifying cell
is able to operate pathways producing one of two lines
of behaviour (e.g., attack, retreat),

3)   Signals of results, indicating whether the effect of
the action was favourable (e.g. food producing) or
unfavourable (e.g. pain producing),

4)   Memory systems by which the signals of results
appropriately alter the probability of the two pathways.

In the octopus the lobes responsible for each of these
stages have been identified and something is known of the
cell types that are involved.   The most obscure is,
unfortunately, the last, which is the most interesting.

This report provides a summary of the system proposed,
indicating the especial contributions made in the past year.

2.   Classifying Systems.

In previous reports evidence has been given that
octopuses analyse shapes in part by evaluating the extent of
their vertical and horizontal contours (Sutherland).   Cells
have been found in the optic lobes with dendritic fields
extended in these directions and it is likely that excitation

of each of these may produce either attack or retreat.
There is an initial slight bias to attack and an octopus
will make a slow exploratory attack on an unfamiliar
object moving in the visual field.   If the attack yields
food it will be repeated, with progressively shorter
latency.

     Some implications of this hypothesis of coding have
been explored in the past year by studying the interference
produced by one pair of figures (say Z and W) on the learning
of a discrimination involving partly similar orientations
(e.g., horizontal and vertical rectangles).   The inter-
ference was found to occur as would be expected if the
classifying system consists essentially of neurons able to
respond to vertical or horizontal contours (Parriss 1963).
However, various interpretations are possible and much
further experiment is needed to prove that the hypothesis is
correct.   Micro-electrode recording is especially
desirable.   Cells of essentially this type have, of course,
been shown by Hubel and Wiesel in the cat.   Further
anatomical work has shown that cells with orientated
dendritic fields essentially similar to those of octopuses
occur in the striate cortex not only in cats but in rats and
monkeys (Colonnier 1963).

3.   Functions of the signals of results of action

     The chief clarification during the past year's work
has been in the study of the systems that signal the results
of action ('pleasure' or 'pain').   Anatomical studies and
surgical removals have shown the plan of the vertical lobe
system and the part it plays in learning and "motivation".
This complicated matter may be understood if we consider
that impulses signalling "food" or "pain" must be present
and perform the following functions if an exploratory homeostat
is to operate properly:

1)   They must operate reflex actions (e.g., swallowing, withdrawal from a hot object)

2)   They must alter the tendency to take further actions: the system must be encouraged by success (but not to the point of "rashness") and made cautious by pain (but not made so "depressed" that there is no further exploration). Such changes alter what is loosely called "motivation". In this they must co-operate with the receptors that indicate the "needs" of the system.   The hunger system of the octopus is at present under investigation.   The animals continue to eat after taking very large amounts of food.   They stop only after taking about 10% of the body weight of fish, and then soon resume.

3)   The third, and perhaps most interesting function of the signals of results, is that they must "teach" the memory system.   To do this they must provide some sort of record of the results of the actions that followed the stimulation of particular members of the set of classifying cells.

4.   Control of "Motivation" by balancing food and pain signals

The proper balance is achieved in octopus by pairs of centres in series.   In the first of each pair a few signals from the lips (taste) are able to activate many cells.   This multiplication of signals thus 'amplifies' the tendency of taste signals to produce further exploration and attack (Maldonado 1963).   The lobe will be called an "amplifier" but, of course, in the sense of multiplying signals rather than amplifying individual ones.   The axons of the cells of this lobe then proceed to the second lobe of the pair, where they are further able to activate many cells. There is, however, another input to this second lobe, presumed to be of nocifensor (pain) fibres and able to switch off the circuit.   The output of the second lobe increases the tendency

to attack. The device thus serves to signal "attack unless pain signals occur".

In the octopus visual system there are two sets of pairs of lobes, placed in parallel one above the other. The visual and taste signals go to amplifier I (lateral superior frontal), whose output goes to amplifier II (subvertical), which also receives pain fibres. The output of II goes back to the optic lobes. After any interruption of this "lower" circuit the octopus no longer launches out to attack an object moving at a distance. But it is not 'blind' and will seize a crab placed near. This lower circuit is thus needed if the visual signals are to be able to produce an attack.

The first lobe of the upper circuit, amplifier III (median superior frontal) receives the same signals as I and sends them to IV (vertical) whose output goes both to I and II. After interruption of the upper circuit the attacks at a distance can be made but they are irregular, and often slow. The results differ according to which lobe was removed. After removal of amplifier III the animals in general attack less; after removal of IV they attack more often.

5. Failure to "read-in" and "read-out" from the memory

Moreover, after either removal the animals failed to perform correctly tasks learned before operation and they only slowly learned new ones. This shows the third of the functions of the signals that indicate the results of action, namely to teach the cells of the memory system which actions should be repeated. It was at first thought that the errors made after removals indicated that the memory store itself had been removed. This is conclusively disproved by the fact that the animals can perform correct discriminations under suitable circumstances. Thus they can discriminate between objects shown simultaneously, or in tests at which no food

reward or shock is given (Muntz, Sutherland and Young
1962). The errors made after operation are due to the
fact that the animals are too greatly influenced by
whatever food or pain they have recently received. They
react to these antecedent stimuli rather than to the
indications in their memory store. We may thus say that
they fail to "read-out" from the memory. They are also
very slow at setting up new representations and we may say
this is a failure to "read-in" to the memory. Their
function in this process of reading-in is probably double.
First they spread the signals of results so that they
arrive at all parts of the memory. This is done by
elaborate plexiform arrangements. Secondly they may
serve to bridge the delay between the time when the
visual signal occurs and the classifying cells are made
active, and the arrival of the signals of results (food
or pain). The vertical lobe system, of course, leads
from the optic lobes and back to them again and we may say
that this circuit serves to maintain the "address" of the
appropriate cells in the optic lobe and then to deliver
the signals of results to the correct "address". (The
differences between digital computers and brains are such
that such terms as "reading in" and "addressing" are only
partly valid). This function of "addressing" is shown
clearly by the fact that, in animals without vertical lobes
there is a no transfer of training from one optic lobe to
the other (Muntz). However, not all the experimental
evidence shows that the vertical lobe system is involved
in delayed responses. Dilly has shown during the last
year that octopuses without vertical lobes can make correct
choices between two alternatives up to half a minute after
relevant cues had been removed. They were not inferior to
normals in this behaviour. Further work on delayed response
is proceeding.

6. **Pairs of centres in tactile and visual learning**
    systems

The validity of the interpretations of these centres
has been greatly strengthened by the realisation that the
octopus contains two largely independent systems for
appropriately balancing and addressing the signals of results.
It is now realised that the tactile learning system studied
by Wells also contains fo r lobes, arranged on the same plan
as those of the visual system.   They are rather smaller
and less sharply demarcated in the tactile sy tem, perhaps
corresponding to the lesser delay between touching an object
and tasting it.   In the cuttlefish and squid, which shoot
the arms at the prey, the delay is minimal and the four touch
centres are n t developed.

7. **Signals of Results and Distance Receptors in Mammals**

The general proposition that emerges is that w e e an
animal uses distance receptors it will need systems to
amplify and balance the signals of results and to deliver
them to the correct addresses in the memory.   This
interpretation may help in understanding the mammalian
forebrain.   Self-stimulation experiments have shown that
centres for 'reward' and 'pain' lie near together in the
hypothalamus.   This is also the region from which complex
motor patterns can be elicited (e.g., feeding, rage, sexual
behaviour).   This region is linked through the anter or
thalamus with the cingulate cortex and hippocampus.   This
circuit has long been known to be concerned with emotion and
'motiv tion' (Papez).   Moreover, the symptoms of both
Korsakov's syndrome and hippocampal removal show that the
circuit is needed for "reading-in" to the memory.   It may
be forecasted th t there are connections not yet discovered
between this circuit and the neocortex.

8.   Excitatory and Inhibitory Synaptic Systems

The 'amplifiers' in octopuses that increase and
decrease the probability of attack have very different
structures both with light and electron microscopy.
The vertical lobe ("inhibitory") contains large numbers of
minute cells with no long axon (amacrines).   These cells
make synapse with the incoming fibres from the "excitatory"
lobe, but there are vesicles on both sides of the synapse
(Gray and Young, 1963).   In fact the amacrine cells then
proceed immediately to make synapse with a third type of
fibre, presumably the output fibres of the lobe.   Although
the full details are not clear, this suggests a mechanism
of pre-synaptic inhibition, especially interesting in view
of the "suppressor" effects that may be exercised by the
lobe.   The "excitatory" amplifier (median superior frontal)
contains no amacrine cells and no synapses with vesicles on
both sides.   Work on these and other lobes is proceeding.
There are great possibilities for associating detailed
knowledge of the synapses with microelectrode recording.

9.   The nature of the neural memory

It is clear that the visual memory cells of Octopus
lie in the optic lobes, probably in the central cell islands.
Electrical stimulation here produces varied motor responses
(Boycott and Young).   The nature of the memory change
remains as obscure as ever.   As an hypothesis we put forward
that each memory cell is connected with one type of
classifying cell (say for horizontal contour) and can
produce one of two outputs (attack, retreat).   After
"horizontal" has occurred, the appropriate cells are kept
at a lowered threshold by the vertical lobe circuit.   If
"food" later occurs, then the pathway leading from the
"horizontal" cell to "retreat" is closed.   The agents
suggested for this process are the small multipolar cells

that accompany the large cells of the central islands of
the optic lobes.   They may have suppressor functions
similar to those of the amacrines of the vertical lobes.
Their especial feature may be RNA systems triggered to
produce sudden changes in enzyme systems, inhibiting one
pathway upon appropriate stimulation and then closing it
altogether by metabolic change or "growth process".
This would agree with Hydén's suggestion of a connection
between RNA and neural memory systems but not that specific
nucleotides code for individual items in the memory.   In
our system the specific information is recorded by selection
from a pre-set code provided by the classifying cells.

As an hypothesis we suggest that each unused pathway
is closed completely by an explosive process when the other
pathway is used.   Learning then consists in the accumulation
of sufficient cells with only one pathway for consistent
decisions to be made.   Others prefer to think of a gradual
change in each pathway.   In either case it is important
to pay attention to the change that occurs on each occasion
of learning.   Study of the accumulation is, in a sense,
of secondary importance.

There is enough evidence to suggest that the whole
learning system of the octopus may operate somewhat as
postulated.   However, much is speculative and much
no doubt, wrong;   there are immense gaps, and years of work
will be needed to fill them.   It may be that mammalian
learning also consists of decisions between the two possible
outcomes of a series of alternative pathways, on a basis of
a system of signals of the results of the exploratory actions
initiated.

10.   B.B. Boycott

Further preliminary investigations assisted by the
grant were made by Mr. B. B. Boycott.   Four kinds of
experiments on Octopus brain were undertaken.

(1) With P.D. Wall, visually evoked potentials were obtained from the **optic** lobes. Potentials were also recorded from the vertical lobe - these were probably evoked potentials but this has not yet been proved with complete certainty. This is the first time such potentials have been recorded in a cephalopod. They are particularly interesting in that the response latencies are very low and the potentials themselves are **complex**. There is a great deal of promise for future experiments here with an ultimate hope of single unit recording.

(2) With E. Florey, biological assays were made of the acetylcholine of precisely located anatomical regions of the octopus brain. These showed that there are very different acetylcholine concentrations in different regions. From as little as 30-50 γ/g. in the superior frontal lobe to as much as 100 and 125 γ/g. in the optic and vertical lobes. A specially suggestive observation was that 4 days after nearly complete de-afferentation of the vertical lobe the acetylcholine concentration appeared to rise (150-170 γ/g.).

(3) Attempts were made to implant electrodes chronically into the brain. These were all torn out by the Octopus when a stimulus was applied. But a good deal of information for improved designs was obtained.

(4) Previous work on lesions to the motor control systems of the brain was extended with particular emphasis on the changes in deficits to be observed with long survival times. Of several results the most interesting was to show that with optico-magnocellular animals the syndrome of a fixed and **rigid** posture changes after a few days and, in time, (about 10 days) very nearly normal locomotion becomes **possible**. This presumably means that the small pieces of **higher** motor centres left in such operations are capable of

reorganisation. Thus, quite complex patterns of behaviour are possible from a small fraction of the total motor centre. Such changes have been observed after damage to mammalian motor systems. They are particularly interesting because reorganisation, of a kind, is characteristic of neural systems concerned with memory. And an understanding of what occurs during such induced changes in a motor system may contribute to interpretations of memory in neural terms.

11. R. L. Gregory

Dr. R. L. Gregory has made a subsidiary investigation relevant to the present one, on the extraordinary telescopic eyes of the copepod Copilia. In these eyes there is a scanning movement performed by the receptor cells. Gregory was able to film this movement and the analysis of the results is providing him with ideas to be further developed this year on the functioning of this and other visual systems.

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